

Should I stay or should I go? The diurnal behaviour of plant-attached zooplankton in lakes with different water transparency

Satu ESTLANDER,* Jukka HORPPILA, Mikko OLIN, Leena NURMINEN

Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

*Corresponding author: satu.estlander@helsinki.fi

ABSTRACT

The role of transparency on the diurnal distribution of plant-attached cladocerans was studied in two similar-sized lakes with contrasting water colour. The diurnal attachment behaviour of *Sida crystallina* (O.F. Müller, 1776) was more pronounced in the less humic lake where the animals remained fixed on plants, indicating that staying attached was a more profitable option. In the highly humic lake, the pattern was opposite, and regardless of time the highest density observed was in the free-swimming individuals, with only few animals attached to the floating-leaves for refuge, indicating that low transparency provided sufficient protection against predation. The attached *S. crystallina* were larger compared to free-swimming individuals in the more transparent lake, suggesting greater vulnerability of large-sized individuals to predation. The results indicate that increasing concentrations of humic substances affecting the light environment may alter the diurnal behaviour and habitat use of plant-attached zooplankton.

Key words: Cladocera; humic lakes; littoral; *Sida crystallina* (O.F. Müller).

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INTRODUCTION

Many prey species resort to refuges to reduce their risk of predation, but usually this is a trade-off between predation risk and optimal feeding conditions (Lima and Dill, 1990; Lima, 1998; Gliwicz *et al.*, 2006). In aquatic ecosystems with predators present, diel vertical migration (DVM) and diel horizontal migration (DHM) of zooplankton are examples of behavioural antipredator defences that are shaped by the trade-off between the favourable energy resources and level of safety (Lampert, 1993; Burks *et al.*, 2002). It has been suggested that in aquatic ecosystems light is the proximate factor triggering the migration of zooplankton in predator presence (Lampert, 1993; Ringelberg, 1995). In DVM, decreasing light intensity triggers the upward movement of zooplankton during dusk (Lampert, 1993). Similarly, horizontal migration is generated by changes in light intensity (Burks *et al.*, 2002), and according to Siebeck (1980) horizontal movement of zooplankton towards open water begins when a part of the optical window seen by the animal is darkened due to elevation of horizon. In lakes with high water colour, light attenuation is strong since dissolved humic substances efficiently absorb light, especially the short wavelengths (Kirk, 1994). Therefore, the concentration of humic substances in the water column affects the overall light intensity, spectral composition and the relative changes in the diurnal light climate (Kirk, 1994; Horppila *et al.*, 2016), and thus inevitably influences the

migratory behaviour displayed by zooplankton (Nurminen *et al.*, 2007). The predation efficiency of planktivores is usually reduced in low water transparency, since most fish depend on vision in prey detection (Vinyard and O'Brien, 1976; Estlander *et al.*, 2012). Additionally, predation is often size-selective and large-bodied zooplankton are more vulnerable (Brooks and Dodson, 1965).

In shallow lakes, littoral areas appear to play an important role in regulating horizontal migration of zooplankton (Lauridsen and Buenk, 1996; Moss *et al.*, 1998). Large free-swimming zooplankton species tend to aggregate within the vegetation beds during daytime to seek refuge among macrophytes against fish predation (Lauridsen and Lodge, 1996; Burks *et al.*, 2002). Compared to free-swimming zooplankton, cladocerans having the ability to attach on substrates may resort to different predator-avoidance strategies (Nurminen *et al.*, 2010). In addition to diurnal migratory behaviour, they can also stay fixed to refuge substrata, such as macrophytes (Quade 1969; Nurminen *et al.*, 2005). Floating-leaved vegetation, often dominating in low transparency waters, appears to harbour considerable densities of plant-attached cladocerans, such as *Sida crystallina* (O.F. Müller, 1776) (Moss *et al.*, 1998). *S. crystallina* is a relatively large Cladoceran species and unlike most plant-associated zooplankton, *S. crystallina* has an anchoring organ (maxillary gland) (Günzl, 1978), which is used to attach to substrate, that secrete a gelatinous glue (Dodson *et al.*, 2001). Nurminen *et al.* (2005) showed a dependency between the density of plant-attached cladocerans and turbidity, underlining

the effect of visibility on the refuge effect of floating-leaved vegetation. The migratory behaviour of periodically plant-attached zooplankton species is poorly known (Moss *et al.*, 1998; Nurminen *et al.*, 2007), and the explanations for benefits of the attachment behaviour of *S. crystallina* are variable. Fairchild (1981) suggested that the attachment of *S. crystallina* is due of considerable energy saving for an organism which must otherwise swim continuously as it feeds. Nurminen *et al.* (2007) showed that attachment of *S. crystallina* may reduce susceptibility to fish predation, and light intensity is the proximate factor regulating the attachment of zooplankton.

To clarify the role of water transparency on the diurnal migration of plant-attached cladocerans we studied the diel attachment pattern of *S. crystallina* in two similar-sized lakes with different concentrations of humic substances and contrasting water colour. We followed the diurnal variation in the density of *S. crystallina* attached to floating-leaved yellow water lily *Nuphar lutea* (L.) Sm. and free-swimming in the water column. We also sampled for the differences in the diurnal variation in horizontal distribution of density of free-swimming *S. crystallina* among and attached to the vegetation. In both lakes, vision-using European perch (*Perca fluviatilis* L., 1758), very common in small humic lakes, is the main planktivore and the primary predator for *S. crystallina* (Estlander, 2011). Additionally, Estlander *et al.* (2010) showed that in less humic lakes, perch fed more on littoral zooplankton, such as *S. crystallina*, than in lakes with higher concentrations of humic substances. Therefore, we hypothesized that the diurnal attachment behaviour of *S. crystallina* is more pronounced in low water colour and higher transparency because of more intense predation threat due to increased visibility. Additionally, in high transparency we expected the amplitude of diurnal horizontal movement to be more pronounced and the large-sized individuals to be more prone to stay attached due to higher vulnerability to predation.

METHODS

The study was conducted in the Evo district (61°13'N, 25°12'N) in two small forest lakes, Iso Valkjärvi and Majajärvi, similar in morphometry (surface area 2.2 and 3.4 ha; mean depth 3.8 and 4.6 m, respectively), and trophic status (total phosphorus 10 and 15 µg L⁻¹; total nitrogen 400 and 600 µg L⁻¹) but different in water colour (50 and 340 mg Pt L⁻¹) and Secchi depth (2.5 and 1 m). Both lakes are inhabited by a perch population (Iso Valkjärvi 1360 ind ha⁻¹, Majajärvi 2600 ind ha⁻¹) (Horppila *et al.*, 2010; Estlander, 2011). Based on long term gill net catches, in Majajärvi the densities of roach (*Rutilus rutilus* (L., 1758) (12 ind net⁻¹) and perch (11 ind net⁻¹) are on a similar level (Horppila *et al.*, 2010). In Iso Valkjärvi the density of roach is very low (0.2 ind net⁻¹). Perch is known to be the

main predator for plant-attached *S. crystallina* (Estlander *et al.*, 2010), whereas roach has been observed to consume *S. crystallina* to a much less extent (Nurminen *et al.*, 2007). The macrophyte vegetation areas in both lakes are relatively narrow, because of the morphological features of the lakes. Macrophyte vegetation of both lakes consists mainly of floating leaved *N. lutea* stands and the density of submerged macrophytes is low (<5% of the vegetation zone) (Estlander, 2011).

To study the diurnal attachment of *S. crystallina*, water samples were taken on 17th July at noon (12:00 hours), at midnight (24:00 hours) and next day, 18th July at noon (12:00 hours). In both lakes, sampling was conducted with a tube sampler (volume 7.1 L) from surface to bottom in three replicate transects from three zones: (A) among floating-leaved *N. lutea* stands, approximately 2 m from shore, (B) from the edge and (C) outside the stands (Fig. 1). The depths of sampling zones were: A=0.8 (± 0.2) m, B=1.5 (± 0.1) m, C=2 (± 0.3) m. The three-replicate sampling transects within both lakes were separated by a 100–200 m distance. Thus, according to the swimming speed of *S. crystallina* (Johansson 1995), sampling transect were independent of each other. Three replicates samples were collected from each zone of each transect. Each replicate consisted of five tube sampler hauls that were assembled into one integrated sample, filtered through a 50-µm net and preserved with formaldehyde. To determine the density of attached *S. crystallina*, three randomly selected *N. lutea* leaves were collected from each sampling transect. Each stem was cut below the water surface and the leaf was rapidly moved into a small container held near (Nurminen *et al.*, 2007). In the laboratory, *S. crystallina* from both water

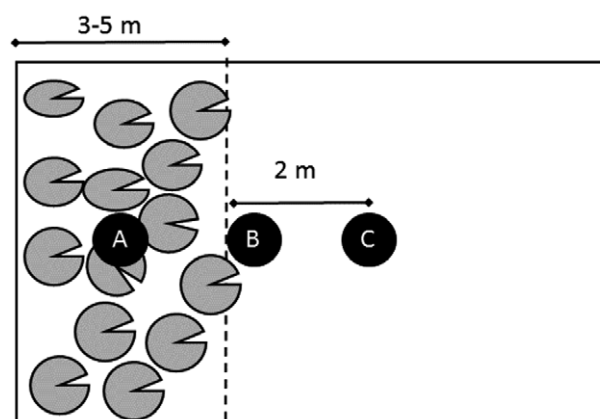


Fig. 1. Sketch of the sampling procedure. Sampling was conducted with tube sampler from surface to bottom in three different sites of lake and from each site, samples were taken from three zones: (A) among floating-leaved *N. lutea* stands, from the edge (B) and outside the stands (C). The depth of sampling zones in three sites per lake were on average: A=0.8 (±0.2) m, B=1.5 (±0.1) m, C=2 (±0.3) m.

column and leaf samples were enumerated and the length (from the anterior edge of the carapace to the posterior edge of the carapace) of 40 randomly selected individuals per each sample measured.

In both lakes, samples for chlorophyll-*a* were taken each sampling time among the vegetation and outside the stands, and filtered through Whatman GF/C filters and analysed spectrophotometrically after extraction with ethanol. Temperature and dissolved oxygen concentration were measured with a YSI-6600 (YSI Inc., Yellow Springs, OH, USA) and light intensity with a LI-1400 datalogger with quantum sensors (LI-COR Biosciences, Lincoln, NE, USA). Light attenuation coefficient was calculated from light intensity measurement from the surface (1 cm below water level) and at 1 m depth. Light attenuation was calculated by the formula:

$$I_z = I_0 e^{-kz} \quad (\text{eq. 1})$$

where I_z is light intensity at depth z , I_0 intensity below the water surface, k attenuation coefficient, z depth.

The density (% coverage) of *N. lutea* was estimated using a 1 m² frame (five replicates) from each sampling sites of lake and the surface area of the lake covered by the macrophytes was measured using GPS in the first day of sampling.

Statistical analyses

The coverage (%) of *N. lutea* at each sampling transect and lake were compared with analysis of variance (ANOVA) (arcsin \sqrt{x} -transformed data). Differences in population densities and size-structure of *S. crystallina* between lakes were compared with analysis of variance for repeated measurements (ANOVAR). The diurnal variations in the density of *S. crystallina* (ind m⁻²) in the water column and attached to leaves in the two lakes were compared with ANOVAR. Additionally, the between-lake diurnal variations in the horizontal distribution of the free-swimming *S.*

crystallina (ind m⁻²) were assessed using ANOVAR. Before the analyses, the datasets were checked for normality and $\ln(x + 1)$ - transformed if necessary. The paired sample *t*-test was used to compare within-lake differences in the length of attached and free-swimming *S. crystallina*. A logistic regression model was used to analyse whether the probability of *S. crystallina* attachment behaviour is dependent on length:

$$y = \exp(\alpha + \beta L) / [1 + \exp(\alpha + \delta L T)]^{-1}$$

where y is the attachment of *S. crystallina* on the *N. lutea* leaf recorded as 0 (not attached) or 1 (attached). L = *S. crystallina* length, and α , β , and δ are parameters. The statistical analyses were performed using SYSTAT ver. 15.0 (SPSS Inc.).

RESULTS

Temperature (18°C Iso Valkjärvi; 20°C Majajärvi), oxygen concentration (8 and 7 mg L⁻¹, respectively) and chlorophyll *a* (7 and 9 µg L⁻¹), did not show significant differences between lakes, sampling sites or sampling times. The vertical light intensity profile varied considerably between the lakes, in Iso Valkjärvi at 1 m depth 15% of surface light was remaining, whereas in the highly humic Lake Majajärvi at corresponding depth only 2% prevailed, and the corresponding light attenuation coefficient values was 0.015 cm⁻¹ in Iso Valkjärvi and 0.03 cm⁻¹ in Majajärvi. The coverage of macrophytes from the total lake area was higher in Iso Valkjärvi (25 %) than in Majajärvi (12 %), but the coverage of *N. lutea* in each sampling transect (average 62 %) showed no significant variation within or between lakes ($P > 0.05$).

There was a significant interaction between time of day, water colour and attachment of *S. crystallina* (ANOVAR: time x water colour x attachment: $F_{2,19} = 5.51$, $P = 0.013$) (Tab. 1; Fig. 2). Regardless of time, in less

Tab. 1. Results from repeated analysis of variance: *S. crystallina* density=time (three levels) x water colour (two levels) × attachment (two levels).

Source	DF	SS	MS	F	P
Water colour	1	26.95	26.95	36.42	<0.001*
Replicates (water colour)	4	1.08	0.27	0.36	0.831
Time	2	0.77	0.39	0.52	0.602
Attachment	1	5.04	5.04	6.81	0.017*
Water colour*time	2	1.91	0.95	1.29	0.299
Water colour*attachment	1	83.37	83.37	112.68	<0.001*
Time*attachment	2	0.72	0.36	0.49	0.622
Water colour*time*attachment	2	8.15	4.08	5.51	0.013*
Error	19				

*Significant at $P < 0.05$.

humic Iso Valkjärvi the density of attached *S. crystallina* (all data pooled) was higher (9600 ± 1450 SE ind m^{-2}) compared to free-swimming density (1100 ± 240 SE ind m^{-2}). In Majajärvi, the opposite phenomenon was observed the majority of individuals being free-swimming (4900 ± 1400 SE ind m^{-2}) and with a very low density of plant-attached individuals (80 ± 20 SE ind m^{-2}) (Tab. 1; Fig. 2). There was a decrease in attached and an increase in free-swimming *S. crystallina* from day to night in Iso Valkjärvi, whereas no clear trend in free-swimming individuals was observed in Majajärvi (Fig. 2). Time or attachment alone were not significant (ANOVAR: $P > 0.05$), thus suggesting that the overall population densities were constant within both lakes during the whole study period. However, the overall density of *S. crystallina* population was higher in Iso Valkjärvi than in Majajärvi (Tab. 1). The density of free-swimming *S. crystallina* increased during the night time in both lakes (ANOVAR time: $F_{4,24} = 5.79$, $P < 0.01$; Fig. 3). In Majajärvi, the average density of free-swimming individuals was higher among vegetation than in the other zones (Fig. 3), but in Iso Valkjärvi no differences between zones were observed (ANOVAR: water colour \times habitat: $F_{4,24} = 1.01$, $P = 0.42$). The interaction term time \times habitat \times water colour was not significant (ANOVAR: $P > 0.05$), suggesting that the diurnal behaviour of free-swimming *S. crystallina* was similar in both lakes (Fig. 3). The average length (940 ± 20 SE μm) of *S. crystallina* did not vary between lakes (ANOVAR: $P > 0.05$). However, the attached *S. crystallina* individuals

were larger than free-swimming individuals (t -test: $P = 0.01$) in Iso Valkjärvi. In highly humic Majajärvi, no size difference was detected between attached and free-swimming individuals (t -test: $P > 0.05$). However, the probability of *S. crystallina* to attach to *N. lutea* leaves was dependent on *S. crystallina* length (logistic regression analysis: $P < 0.001$) as larger individuals had a greater tendency to be attached in both lakes. In addition, the probability of attachment of small and average-sized (400 – 1200 μm) *S. crystallina* was higher in low water colour than in high water colour (Fig. 4).

DISCUSSION

Corroborating our hypothesis, the attachment behaviour of *S. crystallina* was more pronounced in the less humic Iso Valkjärvi, where the animals showed a distinct pattern by mostly remaining fixed on plants regardless of time, indicating that staying attached to vegetation was a more profitable option. When habitats plenty with resources are most dangerous due to predation, *S. crystallina* must choose between food acquisition and mortality risk (Lima and Dill, 1990). The majority of the *S. crystallina* in Iso Valkjärvi were attached to plants due to the high predation risk, but a nocturnal decrease in attached animals and increase in free-swimming animals was observed, indicating diurnal habitat change from the sheltering vegetation to feeding in the water column at night.

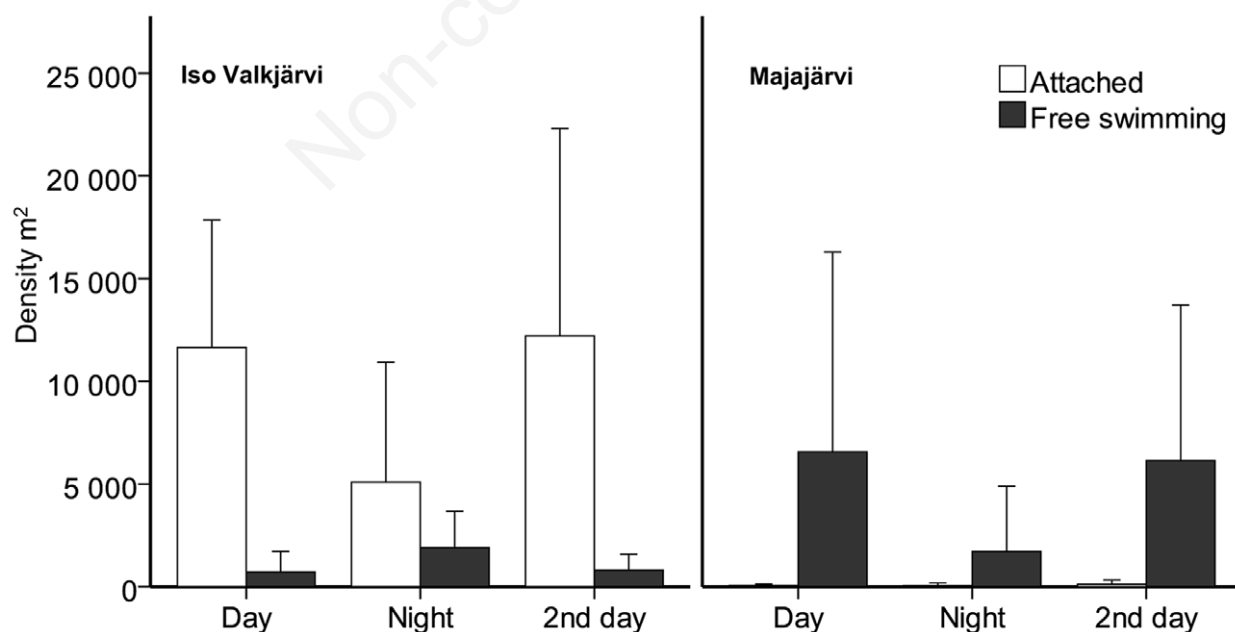


Fig. 2. Diurnal variation of *Sida crystallina* density (ind m^{-2}) attached (white bars) and free-swimming (black bars) in Iso Valkjärvi (50 mg Pt L^{-1}) and Majajärvi (340 mg Pt L^{-1}) ($\pm 95\%$ confidence limits).

The pattern was the opposite in the highly humic Majajärvi. The study included only one diurnal cycle, but numerous aspects confirmed that the between-lake difference in the behaviour of *S. crystallina* was due to the difference in water quality and the diurnal behaviour of cladocerans is rather persistent (Haney and Donald, 1975). In Majajärvi, the highest density was always observed in the free-swimming individuals among vegetation, with only few animals attached to the floating-leaves for refuge. Apparently, low transparency due to high water colour together with the shadow of the floating leaves provided enough protection against predation and thus, *S. crystallina* could remain free-swimming. The animal prefers suspension feeding (Downing, 1981) which is more efficient in the swimming mode moving in the water column than in a sessile mode while attached. In contrast to Fairchild (1981) but in line with Nurminen *et al.* (2007, 2010) the distinct diurnal variation in *S. crystallina* attachment behaviour in contrasting water colour underlines the proximate role of light.

Both resources and predation interact and can have effects on herbivorous zooplankton (Nicolle *et al.*, 2011). However, in humic lakes interspecific competition for food among zooplankton is usually less important in determining the zooplankton community than predation (Masson and Pinel-Alloul 1998). For example, the heterotrophic flagellates can play an important role as a food resource for zooplankton especially in humic lakes (Salonen and Hammar, 1986). Therefore, the available food

resources potentially differed between studied lakes, since they differed distinctly in water colour. However, Geller and Müller (1981) suggested that *S. crystallina* is unable to feed on suspended bacterial cells due to their coarse filter meshes. Here, the chlorophyll *a* concentration did not show diurnal, spatial or between-lake variation, but predation pressure most likely varied between lakes. Fish density in the highly humic Majajärvi was considerably higher compared to the less humic Iso Valkjärvi, indicating that the prevailing free-swimming mode in high water colour was not due to lack of predation pressure. On the contrary, *S. crystallina* remained free-swimming despite the higher predation pressure, which is in line with Estlander *et al.* (2009), who showed that the importance of the littoral zone as a refuge for zooplankton decreases with decreasing transparency. The darker water colour the less fish tend to feed on littoral zooplankton species or macrophyte-associated benthic macroinvertebrates (Estlander *et al.*, 2010).

In Iso Valkjärvi, the nocturnal densities of free-swimming *S. crystallina* were overall higher than those observed in daytime, indicating that in clear water swimming in the water column was safer in the darkness. In contrast, in the highly humic Majajärvi there was a density peak underneath the floating leaves, supporting the assumption that low transparency and shadow of the leaves together provided sufficient shelter for the animals to remain free-swimming at daylight (Nurminen *et al.*, 2007). Planktivores can most efficiently detect zooplank-

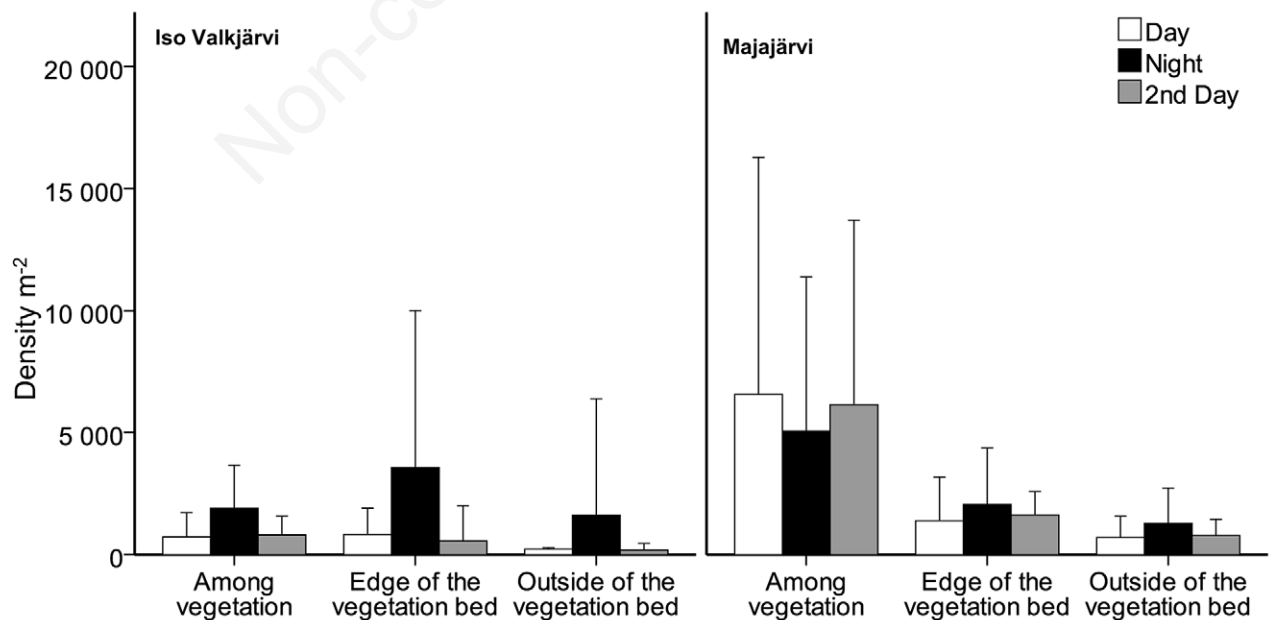


Fig. 3. Horizontal distribution of free-swimming *Sida crystallina* density (ind m⁻²) during day (white and grey bars) and night (black bars) in Iso Valkjärvi (50 mg Pt L⁻¹) and Majajärvi (340 mg Pt L⁻¹) (±95% confidence limits).

ton individuals outside Snell's window or the boundary of the window (at an angle $\geq 48.6^\circ$), where light has been reflected from the surface and comes from the water underneath the fish (Janssen, 1981). The floating leaf covers the window, and a predator outside the leaf has a raised contrast perception threshold, making it difficult to detect a shaded target (Helfman, 1981). Therefore, predation risk in the shade of the floating leaf is lower than in the open water under the same light environment. The leaf cover also affects the spectral composition of light because the floating leaves absorb short wavelength light whereas long wavelengths penetrate the leaves more efficiently (Nurminen and Horppila 2006). In high water colour, together with the overall shading effect decreasing visibility, the spectral composition underneath the leaves may not be optimal for visual predation, because for example perch has low sensitivity for wavelengths >700 nm (Cameron 1982) dominating under the leaf (Nurminen and Horppila, 2006). In addition, the prevailing side-welling light under the leaf cover hampers prey detection by fish (Lythgoe, 1980).

When comparing the free-swimming and plant-attached modes of *S. crystallina*, their difference in vulnerability to predation is imminent. When fish prey on attached individuals, instead of a three-dimensional visual field they face a flat two-dimensional visual field where the prey is harder to detect (Ware, 1973; Nurminen *et al.*, 2010). Fairchild (1982) reported largemouth bass (*Micropterus salmoides* Lacépède, 1802) to make the choice to attack from 1 cm distance while predating on attached *S. crystallina*, and Nurminen and Horppila (2006) found decreasing visibility to shorten the attack distance of perch predating on *S. crystallina* attached to *N. lutea*. Additionally, prey that are stationary and attached to a surface are

generally less prone to detection by predators than freely moving objects (Ware, 1973).

Fairchild (1981) suggested that larger *S. crystallina* had a greater tendency to remain in attached position than smaller individuals due to higher energy loss while swimming. Accordingly, in our study the attached *S. crystallina* individuals were larger, but only in the less humic Iso Valkjärvi. This indicates that in good visibility larger individuals are more vulnerable to predation and choose to stay attached, since vision-using fish, such as perch, select positively for the large-sized cladocerans (Estlander *et al.*, 2010), and transparency is shown to affect size-selectivity of planktivores (Vinyard and O'Brien, 1976). In addition, large female cladocerans that carry eggs are more visible, and thus easy targets for fish (Gliwicz and Pijanowska, 1989). Our results are also in line with the finding that juvenile *Sida* swim better and more frequently than adults (Fairchild, 1981). The causal relationship between size and attachment may be ambiguous, since the dominance of smaller free-swimming *S. crystallina* over attached individuals in less humic Iso Valkjärvi may also be due to size-selective fish predation or the tendency of small-sized individuals to show less antipredatory responses, such as attachment. However, the logistic regression showed that water colour affects the length at which *S. crystallina* individuals prefer the attached mode. In high transparency, the individuals attach to the floating leaved surface at a smaller size than in low transparency.

CONCLUSIONS

In aquatic ecosystems, the level of safety for zooplankton is usually linked to the vertical or horizontal dimension of the habitat (Werner and Gilliam, 1984; Clark and Levy, 1988), but also the prevailing light environment is important, because prey capture of planktivorous fish is mainly based on vision (Vinyard and O'Brien, 1976; Taylor, 1980). During the last decades, lakes in Northern and Central Europe have undergone an increase in dissolved organic carbon concentrations, resulting in decreasing visibility and brownification of waters (Vuorenmaa *et al.*, 2006). Our study suggests that increasing concentrations of humic substances that affect the light environment underwater may alter the diurnal behaviour and habitat use of plant-attached zooplankton in lakes with predation pressure.

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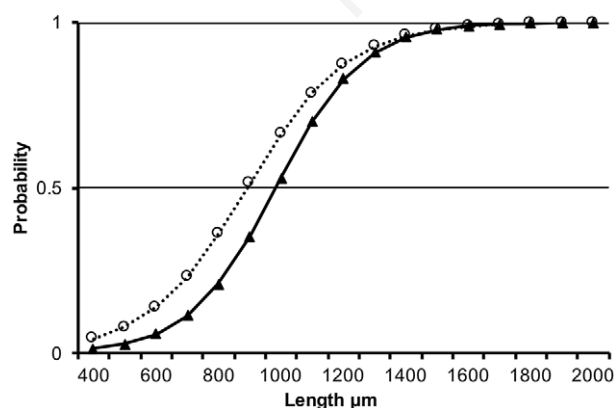


Fig. 4. Probability of attachment of *Sida crystallina* to *Nuphar lutea* leaves against *Sida crystallina* length estimated with logistic regressions in low (50 mg Pt L^{-1}) (dotted line) and high (340 mg Pt L^{-1}) (solid line) water colour.

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